SANDAKANIA 21 (2016): 21–64

A taxonomic treatment of the Asiatic allies of *Rothmannia* (Rubiaceae: Gardenieae), including the new genera *Ridsdalea* and *Singaporandia*

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Summary. *Rothmannia* was formerly considered a highly variable genus ranging from Africa to mainland Asia and the Malay Archipelago. The central taxonomic problem had been the difficulty in reconciling morphological variation among key groups of taxa, namely a core group including the African type, or *Rothmannia* Thunb. *sensu stricto*, that has corolla lobes overlapping to the right (a comparatively rare and distinctive condition in the Rubiaceae generally) *vs* other African and all Asian-Malay Archipelago taxa that have corolla lobes overlapping to the left. Also, the array of taxa from Africa into Asia and beyond has corolla forms ranging from infundibular and campanulate to hypocrateriform, and mere division based on corolla type still included other highly variable characteristics. Recent molecular phylogenetic analysis of *Rothmannia sensu stricto* and allies has unequivocally demonstrated distinct clades correlated with unique, possibly synapomorphic, morphological states among the alliance members in Africa. The Asian-Malay Archipelago taxa together form a separate major clade, but further resolution within the group could not be obtained with only some 30% taxa sampled using only a few DNA regions. However, the availability of a rich spectrum of morphological evidence recently obtained can now be used to support a morphological classification of the Asiatic taxa based on floral characteristics including corolla form and pollen characteristics, as well as plant architecture and other characters. Of the three genera recognized, *Kochummenia* K.M.Wong is distinct by its subhypocrateriform corolla with linear lobes exceeding the tube, anthers inserted near the tube base and leaf epidermal cells with deeply sinuated anticlinal walls, which are clearly synapomorphic characters defining a genus so far known only from the Malay Peninsula. The new genus *Ridsdalea* J.T.Pereira

& K.M.Wong is characterized by a hypocrateriform or campanulate corolla and reduction of only one member of the distal leaf pair on a 2-node branch module, resulting in a trifoliate leaf cluster formed with the proximal leaf pair. *Ridsdalea* is widespread with c. 30 species, through mainland Asia and the Malay Peninsula into East Malesia. The newly described genus *Singaporandia* K.M.Wong is monotypic, based on *Rothmannia* (*Randia*) *macrophylla*. It is distinguished by an infundibular corolla, exceptionally long anthers with large pollen and ectocolpus, and complete reduction of the distal leaf pair on a 2-node branch module; it is distributed in the Malay Peninsula including Singapore, and Sumatra. *Kochummenia terengganuensis* K.M.Wong is newly described and the necessary taxonomic combinations into *Ridsdalea* are effected for 25 published taxa across tropical and subtropical Asia and Malesia. A number of lectotypifications and neotypifications are designated.

Rothmannia Thunberg was first described in 1776 after Georgius Rothman (1739–1778), a Swedish physician and botanist. Its type species is the South African *Rothmannia capensis* Thunb. Over 70 published binomials for *Rothmannia* have been documented in the International Plant Names Index (IPNI 2016), representing taxa from tropical and subtropical Africa, the Seychelles, Myanmar, Thailand, Cambodia, Laos, Vietnam, the Andaman Islands, South China, the Malay Peninsula, Java, Sumatra, Borneo and Papua New Guinea. Out of these, 14 binomials have been described for parts of Malesia (Fagerlind 1943, Bremekamp 1957, Tirvengadum 1983; Wong 1984, 1989; Pereira & Ridsdale 2012) (see also Puff & Wong 1993). Although Wong (1984) reviewed the whole assemblage of *Randia* s.l. for Peninsular Malaysia and segregated *Rothmannia* as a genus, a complete revision for Malesia has not been made.

A HISTORICAL PERSPECTIVE OF *ROTHMANNIA*

The delimitation of *Rothmannia* had been superficial and contentious. In earlier times, several species that were transferred to *Rothmannia* had been included in the broad concept of *Randia* in the "classical" Gardenieae, as *Randia* sect. *Euclinia* in De Candolle (1830), Hooker (1873), and Schumann (1891); *Randia* sect. *Gardenioides* in Hooker (1880); and *Randia* sect. *Grandiflorae* in Ridley (1923). In that "classical" view, *Randia* was in fact a heterogeneous pantropical genus (Fagerlind 1943, Wong 1984). The genus *Randia* Houst. ex L. was originally described with two species, *R. mitis* L. and *R. aculeata* L. Although in 1929, Hitchcock & Green had lectotypified the genus with *R. mitis*, a New World species, *Randia* spp. were generally supposed to share only a few common characters, viz., bisexual flowers with contorted corolla lobes; bilocular fruits that are indehiscent or irregularly splitting, with each locule containing many compressed or angular seeds, allowing a loose interpretation worldwide. Many *Rothmannia* species had been placed under *Randia* s.l. in floras and checklists by Oliver (1877), King & Gamble (1903), Merrill (1921), Pitard (1923), Hutchinson & Dalziel (1931), Craib (1932), Masamune (1942) and Backer & Bakhuizen (1965).

In some cases, species later considered to be better accommodated within *Rothmannia* had been originally placed in *Gardenia* s.l., e.g., *Gardenia* **s**ect. *Rothmannia* in Endlicher (1838), Hooker (1873) and Schumann (1891), and also in floras and checklists by Miquel (1856), Merrill (1921) and Masamune (1942). As early as 1781, even the type species *Rothmannia capensis* was transferred to the genus *Gardenia,* under the name *G. rothmannia* L.f.*,* by Linneaus in the *Supplementum Plantarum Systematis Vegetabilium*.

The inclusion of such species in *Randia* s.l. and *Gardenia* s.l. had been arbitrarily based on character-states such as bilocular ovaries in defining '*Randia'* and unilocular ovaries in '*Gardenia'*, and also placentation. The difference between the bilocular and unilocular ovaries and their placentation were not reliable characters and created ambiguity for taxonomists in the placement of species in these two genera (*Randia* and *Gardenia* Ellis) when used in isolation. Hutchinson & Dalziel (1931) concluded that "The genera *Gardenia* and *Randia* are in much need of revision and recasting on the lines other than the placentation of the ovary."

Fagerlind (1943) was the pioneer in demonstrating the heterogeneity of *Randia* through the use of characters including branching patterns and pollen grain features. As a consequence, he re-established three genera including *Rothmannia* and made several new combinations in *Rothmannia*, including the New Guinean *Rothmannia macromera* (Lauterb. & K.Schum.) Fagerl. Later, *v*arious authors accepted *Rothmannia* as a distinct genus in Africa, including Keay (1958), Hepper & Keay (1963), Hallé (1970), Dyer (1975), Bridson & Verdcourt (1988), Palgrave (1988), Somers & Robbrecht (1991) and Sonké & Simo (1996). Keay's work greatly influenced taxonomists working on the African and Asiatic Rubiaceae (Tirvengadum 1982). Likewise, a number of Asiatic species have been described or recombined in *Rothmannia*, in Bremekamp (1957) for Laos, Indo China; Yamazaki (1970) for East Asia, Tirvengadum (1982, 1983) for South and Southeast Asia (describing three new species and making three new combinations for *Rothmannia*); Wong (1984, 1987, 1989) for Peninsular Malaysia; and Pereira & Ridsdale (2012) for the Philippines.

In spite of this, and perhaps sensing that a wide range of material was once again being swept into the concept of a widespread genus, Bakhuizen (1975), in his synoptical key to the *Genera of the Rubiaceae of Thailand*, retained Schummann's classification of Rubiaceae based on the character of "single ovule per ovary" versus "more than one ovule per ovary", and treated *Randia* in its widest sense, rejecting the views on segregating the various groups as genera as done by Keay (1958) and other botanists. However, for Thailand, a recent account of the *Rubiaceae of Thailand* by Puff et al. (2005) recognized some eight species of *Rothmannia* in Thailand. Meanwhile, in South China, a new species *Rothmannia daweishanensis* Y.M.Shui & W.H.Chen was published by Shui et al. (2003). Puff & Wong (1993) presented a synoptic listing of the genera of Bornean Rubiaceae, including mention of several *Rothmannia* species. Coode et al. (1996) listed an unidentified *Rothmannia* in their Brunei checklist. Beaman & Anderson (2004), with the assistance of Pereira, recognized two unidentified *Rothmannia* species for the area around Mt Kinabalu, Sabah. For the Balikpapan-Samarinda area of East

Kalimantan, Indonesia, Kessler et al. (1992) documented a single species of *Rothmannia*, but subsequently a new species was mentioned (but not named) in *Trees of the Balikpapan-Samarinda Area* (Kessler & Sidiyasa 1994).

Although *Rothmannia* has been accepted generally by most taxonomists as an entity distinct from *Randia* and *Gardenia*, a more thorough analysis taking into account both the African and Asiatic species had not been carried out and the limits of the genus itself have become somewhat arguable, as demonstrated through the work of Bremekamp (1957), Keay (1958), Wong (1984) and Bridson & Verdcourt (1988). Keay (1958) had pointed out the occurrence of two types of corolla aestivation within the African species, i.e., corolla lobes contorted to the right in the type species and its allies, and corolla lobes overlapping to the left in the other species. Wong (1984) considered that this kind of variation (right and left contortion of corolla lobes), which also occurs in *Alstonia* R.Br. (Apocynaceae), may have some value in distinguishing infrageneric groups. He recommended a critical examination of both the African and Asiatic *Rothmannia* species to better understand their relationships, as well as to confirm characters that are generically important. Additionally, Wong (1984) also concluded that there did not appear to be a single corolla shape for distinguishing *Rothmannia* as a whole. This can be seen by a range of corolla form, from infundibular and campanulate to salverform (= hypocrateriform) (Wong 1984, Bridson & Verdcourt 1988), found among the species.

There is also a need to consider the relationship between *Rothmannia*, *Kochummenia* K.M.Wong and *Heinsenia* K.Schum., which share some interesting characters. *Heinsenia* is a monotypic African genus that was placed by Robbrecht & Puff (1986) in its own tribe, Aulacocalyceae. Keay (1958) and Bridson & Verdcourt (1988) have pointed out that *Heinsenia* and *Rothmannia* share the same branching pattern and have similar corolla speckling (i.e., white with coloured spots inside). In a phylogenetic analysis using *rbcL* sequence data and a combined cladistic analysis using morphological and molecular data (Andreasen & Bremer 2000), *Heinsenia* emerged as weakly associated with *Rothmannia* (the two emerging as a minor clade with poor bootstrap support). The African *Aulacocalyx* Hook.f. was also placed in the same tribe as *Heinsenia* by Robbrecht & Puff (1986), and in fact at some point, *Heinsenia* was placed as a synonym of *Aulacocalyx* by Petit (1962). Later, *Heinsenia* was even proposed as a subgenus of *Aulacocalyx* by Verdcourt (1981). Both these genera share a small number of seeds, (1–)2–4 per fruit, seed coats that are lacking or strongly reduced, and superior embryo radicals (Robbrecht & Puff 1986). *Kochummenia* (endemic to Peninsular Malaysia) also has the same branch architecture as *Rothmannia*. However, in *Kochummenia*, the corolla form is what we term subhypocrateriform, in having a short tube with linear lobes that are much longer, a feature unique to that genus (Wong 1984, Robbrecht & Puff 1986), whereas in *Rothmannia* s.l. the corolla can be campanulate, infundibular and salverform, but with broad lobes shorter than the tube. A phylogenetic study by Persson (1996), based on morphological characters, demonstrated *Kochummenia* as being distinct from (the African species of) *Rothmannia*.

It is this complex—based around the African concept of *Rothmannia* as accepted by Keay (1958) and subsequent workers, and the associated genera both in Africa (including *Aulacocalyx*, *Heinsenia* and *Phellocalyx* Bridson) and Asia (including *Kochummenia*), as well as a handful of earlier described species that have resemblance to elements within this group but which obviously remain aberrant if maintained within *Randia* or *Gardenia*—that we refer to as the *Rothmannia* taxonomic complex.

RECENT TAXONOMIC INDICATIONS

A number of cladistic studies have addressed classification of higher-level groups in the Rubiaceae, viz., the subfamily Ixoroideae (Andreasen & Bremer 1996, 2000) and the tribe Gardenieae (Persson 1996, 2000; Puttock & Quinn 1999). In these studies, *Rothmannia* was only represented by African species. These studies reaffirmed the notion that *Randia* s.s. is not closely related to many of the genera that have been lumped together as *Randia* s.l. Andreasen & Bremer (1996) analyzed the phylogeny of the Ixoroideae and confirmed that *Randia* s.s. is entirely neotropical, in accordance with the views of previous authors including Bremekamp (1957) and Keay (1958). Also, the position of *Rothmannia* (represented by *R. longiflora* Salisb.) in their cladistic analysis was unresolved. Persson (1996) conducted a cladistic analysis using both morphological and anatomical characters of the Gardenieae based on Robbrecht's (1988) classification. *Randia* s.s. and *Gardenia* s.s. were recovered as sister taxa in one of the major clades (the so-called "tetrad group") in the strict consensus tree of equally parsimonious cladograms, as well as in the strict consensus tree after successive character reweighting. In Persson's analysis, neither *Kochummenia* nor *Rothmannia* was clearly allied to any of the well-supported clades within the Gardenieae group of genera. Andreasen & Bremer (2000) performed a combined phylogenetic analysis using morphology, nuclear and chloroplast DNA data, to assess tribal and generic relationships in the Ixoroideae subfamily. This phylogenetic analysis showed that *Rothmannia* associated weakly with *Heinsenia* but their position was unclear although clearly nested within the Gardenieae. *Heinsenia* had been placed within the Aulacocalyceae by Robbrecht & Puff (1986), so Andreasen & Bremer (2000) suggested that this tribe should be included within the Gardenieae. Persson (2000) performed a molecular phylogenetic analysis (combining *rps* 16 intron and *trn*L-F intergenic spacer sequences) to evaluate the relationship among members of the Gardenieae. In that analysis, *Rothmannia* (represented by members of the type alliance, *R. annae* (E.P.Wright) Keay and *R. fischeri* (K.Schum) Bullock ex Oberm.) was unresolved within a very weakly supported core Gardenieae clade. *Rothmannia* was also included in a supertree analysis (Robbrecht & Manen 2006). These authors stressed, however, that in general, phylogenetic and morphological knowledge of the Gardenieae was still too poor.

The first modern analysis taking into account both the African and Asiatic species of the *Rothmannia* complex was carried out by Pereira (2008), investigating morphological as well as palynological and anatomical characteristics, and offering a morphological phylogenetic

analysis. Pereira (2008) also made a preliminary analysis with 8 taxa using the chloroplast *trnQ-rps* intergenic spacer gene, which demonstrated the clear divergence of an African clade from an Asian clade. However, phylogenetic structure within each of these two main *Rothmannia* groups could not be addressed because of the minimal taxon sampling.

The Gardenieae study of Mouly et al. (2014) showed five statistically well-supported groups: an *Aidia* Lour. group, a *Gardenia* group, a *Porterandia* Ridl. group, a *Randia* group, a *Rothmannia* group, and the monogeneric lineages *Massularia* (K.Schum.) Hoyle and *Schumanniophyton* Harms & R.D.Good. Their *Rothmannia* group indicated *Aulacocalyx* and *Heinsenia* together as a clade, sister to another comprising the genera *Phellocalyx*, *Rothmannia* and *Kochummenia*, with weak support. Subsequent phylogenetic analyses which are being prepared for publication by Mouly et al. (in prep.), using data for three cpDNA and one nrDNA regions, have now confirmed that the *Rothmannia* complex is indeed paraphyletic. These analyses indicate, as earlier shown by Pereira (2008) in a preliminary manner, that the Asiatic allies *Kochummenia*, various species presently named as *Rothmannia*, the species named *Gardenia pseudoternifolia* Valeton, and other unnamed Asiatic taxa generally identified with *Rothmannia* s.l., all fall entirely within their own distinct clade. These Asiatic elements are clearly separate from *Rothmannia* s.s., *Phellocalyx*, the closely allied pair *Aulacocalyx* and *Heinsenia*, and an entire suite of African taxa with left-contorted corolla lobes (Mouly et al. in prep.). Unfortunately, the molecular sampling of the Asiatic taxa has been limited, so that further elucidation of their taxonomy—as taxa outside of the immediate African alliance of *Rothmannia* s.s.—proceeds with the morphological, palynological and anatomical analyses in this paper.

THE ASIATIC ALLIES OF *ROTHMANNIA*

Once the disposition of the African taxa including *Rothmannia* s.s. could be reconciled as an entirely distinct genetic lineage (Pereira 2008, Mouly et al. in prep.), the treatment of the Asiatic allies could proceed uncomplicated by parallels in morphological development found in the African taxa. Our objective in the present paper is to elucidate the major taxa in the Asia-Pacific region based on morphological, palynological and anatomical assessments carried out for a representative number of Asiatic taxa, as well as comparisons with selected African taxa, of the *Rothmannia* complex.

Inflorescence development

The inflorescences in nearly all members of the *Rothmannia* complex (including *Rothmannia* s.s. and *Kochummenia*) are distinctly terminal and typically formed at the end of a branch segment or modular unit consisting of a proximal node with a pair of normally expanded leaves and a distal node with one reduced leaf and one normally developed leaf, i.e., a 2-node segment that carries three leaves at closely occurring nodes (Fig. 1: A1 & A2). Due to the

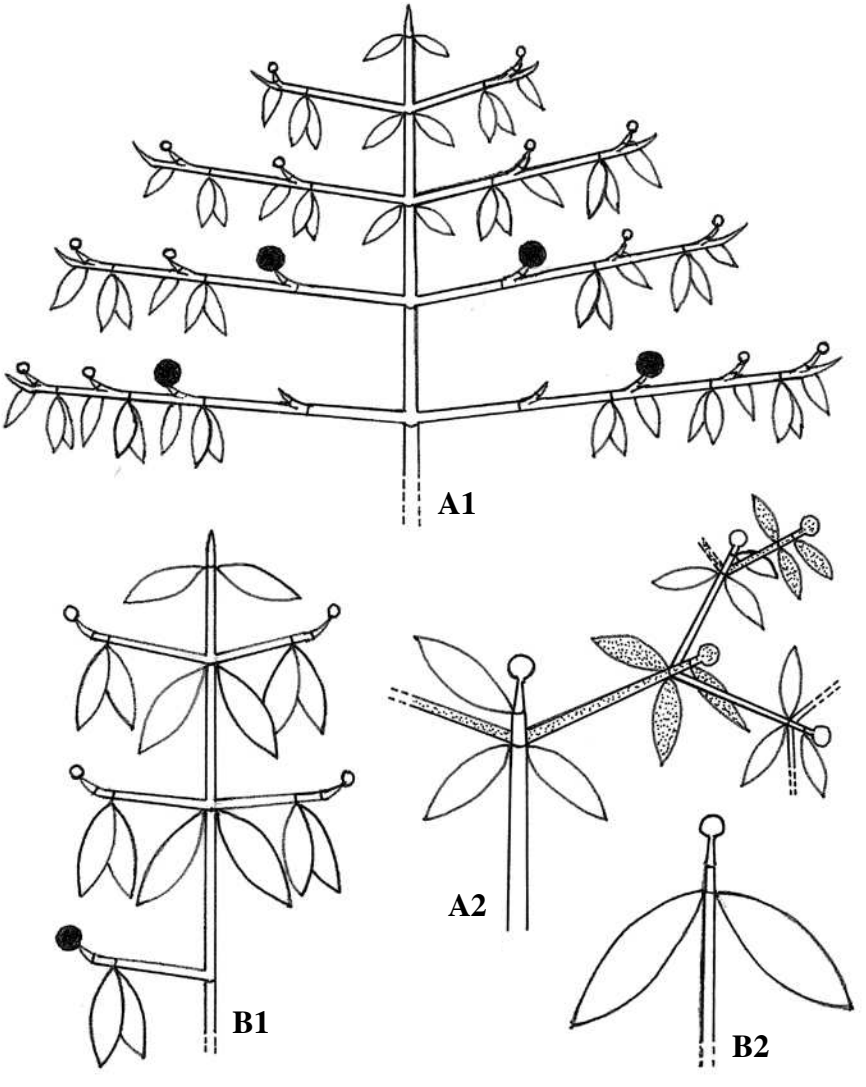

Fig 1. Idealized representations of branch module construction in *Kochummenia*, *Ridsdalea* (previously part of the Asian *Rothmannia* complex) and *Singaporandia* (based on *Rothmannia macrophylla*). The profile view of the plant architecture in *Kochummenia* and *Ridsdalea* (**A1**) shows continuous stem growth and branch production; branching is extended via substitution by successively higher-order modules. The plan view of this branching system (**A2**) shows a succession of branch modules; each branch module consists of an elongate first internode, a proximal node bearing a pair of normal leaves and a second (distal) node with one leaf reduced, presenting a trifoliate cluster. The profile view of plant architecture in *Singaporandia* (**B1**) also shows continuous stem growth and branch production, but the branch module bears a pair of normal leaves only at the first node, with both leaves reduced at the second (distal) node; the primary module is not normally extended; plan view of primary branch module (**B2**) with a single pair of leaves. (Small circles represent inflorescence development; solid larger circles indicate fruiting in older modules.)

displacement to one side during sympodial branch development, the inflorescence sometimes appears to be lateral**.** When they develop, inflorescences or infructescences are produced at the end of the branch segment or module. This was illustrated and highlighted by Bridson & Verdcourt (1988) and simply termed the "*Rothmannia*-type" of branch development. The inflorescences can potentially be produced at the end of every modular unit of an adult plant. In contrast, in *Rothmannia macrophylla* (R.Br. ex Hook.f.) Bremek., the terminal inflorescence is produced following the distal (second) node that has both leaves vestigial (vastly reduced in size), the proximal node bearing a pair of normally developed leaves (Fig. 1: B1 & B2).

It is noteworthy that the species with right-contorted corolla lobes (i.e., the type alliance of *Rothmannia*) always have truly solitary flowers (without any bracteoles on the flower-bearing axis that could represent sites of reduced cyme branches), whereas the African species with left-contorted corolla buds have typically 1-flowered, reduced cymes, although among the latter group, cymes may be (2–)3–5-flowered (in *R. manganjae* (Hiern) Keay and *R. lujae* (De Wild.) Keay) or even much-branched and 3–17-flowered (in *R. engleriana* (K.Schum.) Keay). In the majority of the Asian and SW Pacific species, the inflorescences are typically much-branched with a larger number of flowers, typically more than 3 flowers per cyme (in *Randia anisophylloides* Wernham, there are typically 40–130 flowers). Reduced, 1-flowered cymes may be the only form in some species, e.g., *Rothmannia daweishanensis, R. kampucheana* Tirveng., and *R. thailandica* Tirveng. (all in mainland Asia), or occur together with many-flowered branched cymes (e.g., *Gardenia forsteniana* Miq., *G. pseudoternifolia*; *Rothmannia lagunensis* (Merr.) J.T.Pereira & Ridsdale and *R. merrillii* (Elmer) J.T.Pereira & Ridsdale; and in the mainland Asian species, *Rothmannia sootepensis* (Craib) Bremek. and *R. venalis* Bremek.). Asian species with more than 3 flowers per cyme include *Rothmannia attopevensis* (Pit.) Bremek., *R. eucodon* (K.Schum.) Bremek., *R. sootepensis, R. vidalii* Bremek., and *R. wittii* (Craib) Bremek. In *Rothmannia macrophylla,* the flowers are 1–3 together in a cyme. In *Kochummenia*, the flowers are never solitary and are borne in 3–9 flowered cymes.

Plant architecture: stem growth and branching patterns

Based on the branch and inflorescence development discussed above, the plant architecture so far known of *Rothmannia* complex species can be identified with the models of Petit and Fagerlind as defined by Hallé, Oldeman & Tomlinson (1978). Both Petit's and Fagerlind's models share the following similar key features: an orthotropic main axis and plagiotropic branch development by substitution. The difference between the two models lies in the continuous growth of the stem or trunk axis (in Petit's model) (Fig. 1, 2), as opposed to rhythmic or episodic growth (in Fagerlind's model). *Gardenia grandis* Korth., *G. pseudoternifolia, Rothmannia merrillii* and *R. schoemanii* (Teijsm. & Binn.) Tirveng. (Asia) and *Rothmannia annae* and *R. whitfieldii* (Lindl.) Dandy (*Rothmannia* s.s., Africa) conform to Petit's model, with branches produced at every stem node. *Rothmannia longiflora* appears

Fig. 2. Continuous stem growth and branch production in a young sapling of *Ridsdalea schoemanii* (syn. *Rothmannia schoemanii*). (Photo: J.T. Pereira)

to conform to Fagerlind's model in seasonal Africa (Hallé, 1967, Hallé & Oldeman, 1975, Hallé, Oldeman & Tomlinson, 1978), and to Petit's model when cultivated in everwet Peninsular Malaysia according to our observations, but even in Malaysia, branch production is episodic, as in Africa, with non-branching stem nodes produced between branching episodes. Whereas more observations need to be made and transplants of such species from one environmental regime to another may serve as interesting experiments, it is clear that Petit's and Fagerlind's models are very closely related. Also, *Gardenia grandis* has been documented as having Fagerlind's model in the collector's label for one Sumatran collection of this species (*Laumonier TFB 356*) but this was not the case for a plant we studied at Endau Rompin, Johor, Malaysia. The main stem clearly branches regularly and has continuous growth. In *Kochummenia,* the tree architecture conforms to Petit's model, whereas *Rothmannia macrophylla* shows a somewhat reduced version of Petit's model with successive nodes along the stem axis producing either solitary or paired lateral branches.

In most of the investigated *Rothmannia* and *Kochummenia* spp. (Fig. 1: A1 & A2), the branches are modular, and plagiotropic by substitution, i.e., each module is terminated by the apex becoming inactive or bearing an inflorescence, and then substituted by new modules of a higher order developing from axils of the leaf pair in the horizontal plane (from the proximal node). However, in *Rothmannia macrophylla* (Fig. 1: B1 & B2), the branch system is reduced to a single module typically (with very rare occurrence of a second module indicating the essentially reduced modular construction). Each modular unit in the branch system of *Rothmannia* and *Kochummenia* typically has a proximal long internode (more than 5 times the length of the internode distal to it) with a pair of fully developed

Fig. 3. *Ridsdalea pseudoternifolia* (at first named *Gardenia pseudoternifolia*), detail of branch module apex showing the proximal node with a pair of normal leaves (and a pair of axillary branches from their axils, which are higher-order modules), and the distal node with only a single normal leaf developing. (Photo: K.M. Wong)

leaves at the first node (end of this long internode) and subsequently one short internode with one leaf of a pair reduced and the other normally developed (Fig. 3), just before the terminal bud ceases growth (and sooner or later) producing a terminal inflorescence (Fig. 4). Thus, each branch segment produces two nodes bearing, between them, three expanded leaves (Fig. 1: A2). When these nodes are very close, each branch segment appears to bear leaves in a trifoliate group or cluster (Fig. 3, 4). In the sense of Hallé, Oldeman & Tomlinson (1978), each modular unit is determinate, with complete transformation of the shoot apical meristem into a flowering axis after a period of vegetative growth. Subsequent branch extension by higher-order modular units is continued from either one or both leaf axils at the proximal node (i.e., in the horizontal plane) of the previous module. In all the species observed (except in *Rothmannia macrophylla*), the lateral branches produced from the axils of the primary branch are normally paired and subsequent higher-order branching can either be solitary or in pairs. When a series of higher-order branches are produced solitarily, they can form a zig-zag pattern.

In *Rothmannia macrophylla*, after the production of the proximal long internode in the primary branch axis with a pair of fully developed leaves at the first node, followed by a subsequent node with both leaves reduced (often vestigial and microscopic in size), further growth is typically terminated by inflorescence development (Fig. 1: B2; Fig. 5). Very exceptionally, one or two second-order branches develop from the leaf axils of the first node of the primary branch, and then these second-order branches also bear a pair of normal leaves, a pair of vestigial leaves and a terminal inflorescence.

Fig. 4. A zig-zag series of branch modules of *Ridsdalea pseudoternifolia*, with the two youngest trifoliate leaf clusters intact, and infructescences. (Photo: Suzana Sabran)

Fig. 5. Lateral branch of *Singaporandia* (based on *Rothmannia macrophylla*) bearing a single pair of leaves and a terminal flower. (Photo: Cerlin Ng)

Lower leaf epidermis

The lower leaf micromorphology of the *Rothmannia* complex has been studied by one of us (Pereira 2008). Anticlinal wall outlines of epidermal cells can be categorized into three general types. Type A has straight to gently curved sections of the cell outline, with basically low-frequency, low-amplitude sinuations corresponding to Types 1 and 2 of the system of Stace (1965) and Wilkinson (1979). Type B has pronounced sinuations of higher frequency and low to medium amplitudes, including Types 3, 4 and 5 of Stace and Wilkinson. Type C (Stace's and Wilkinson's Type 6) has pronounced sinuations of high frequency and large amplitudes (i.e., deep sinuations) in addition to these features.

Type A outlines (straight to gently curved) are found in the African species only, viz., *Rothmannia engleriana, R. globosa* (Hochst.) Keay, *R. manganjae* and *R. whitfieldii*. Type B outlines (with pronounced waves of low to medium amplitudes) are by far the most common condition. This type is found in both the Asian taxa, such as *Randia anisophylloides, Gardenia grandis, Rothmannia eucodon, R. schoemanii,* and *R. vietnamensis* Tirveng., as well as the African species, e.g., *Rothmannia capensis*, *R. fischeri* ssp. *morambollae* (Hiern) Bridson, *R. longiflora*, and *R. lujae*. Type C outlines (deep sinuations, i.e. waves with very large amplitudes) are known only in *Kochummenia stenopetala* (King & Gamble) K.M.Wong.

In terms of anticlinal wall outline, *Rothmannia macrophylla* is not specially distinguished from most of the other *Rothmannia* species. However, the anticlinal wall outline in *Kochummenia stenopetala* appears to be unique among members of the complex.

Floral morphology

Corolla form. Four types of corolla form occur in the *Rothmannia* complex (including *R. macrophylla* as well as *Kochummenia*), viz., hypocrateriform (salver-shaped), campanulate (bell-shaped), infundibular (funnel-shaped), and subhypocrateriform with long lobes.

A hypocrateriform corolla is typical of *Rothmannia* complex species in Asia and SW Pacific but is generally not found in African species of the complex except in some species of *Aulacocalyx*. This corolla form is found in, e.g., *Rothmannia macromera* from New Guinea, *Rothmannia merrillii* (Fig. 6A) from Borneo and the Philippines, and *Rothmannia sootepensis* from mainland Asia. The campanulate form occurs commonly among *Rothmannia* complex species in both Africa (*R. annae, R. capensis, R. engleriana, R. fischeri* (ssp. *fischeri* and ssp. *moramballae*), *R. manganjae*, *R. ravae* (Chiov.) Bridson and *R. urcelliformis* (Hiern) Robyns and *R. globosa*) and Asia and the SW Pacific (*R. attopevensis* (Pit.) Bremek., *R. daweishanensis, R. eucodon, R. pulcherrima* (Kurz) Tirveng., *R. schoemanii, R. vidalii, R. wittii* (Fig. 6B), and *Gardenia forsteniana*). In Malesia, the common type of corolla form among *Rothmannia* complex species is hypocrateriform, while the campanulate form is only found in two species, *R. schoemanii* and *Gardenia forsteniana*. The infundibular corolla form

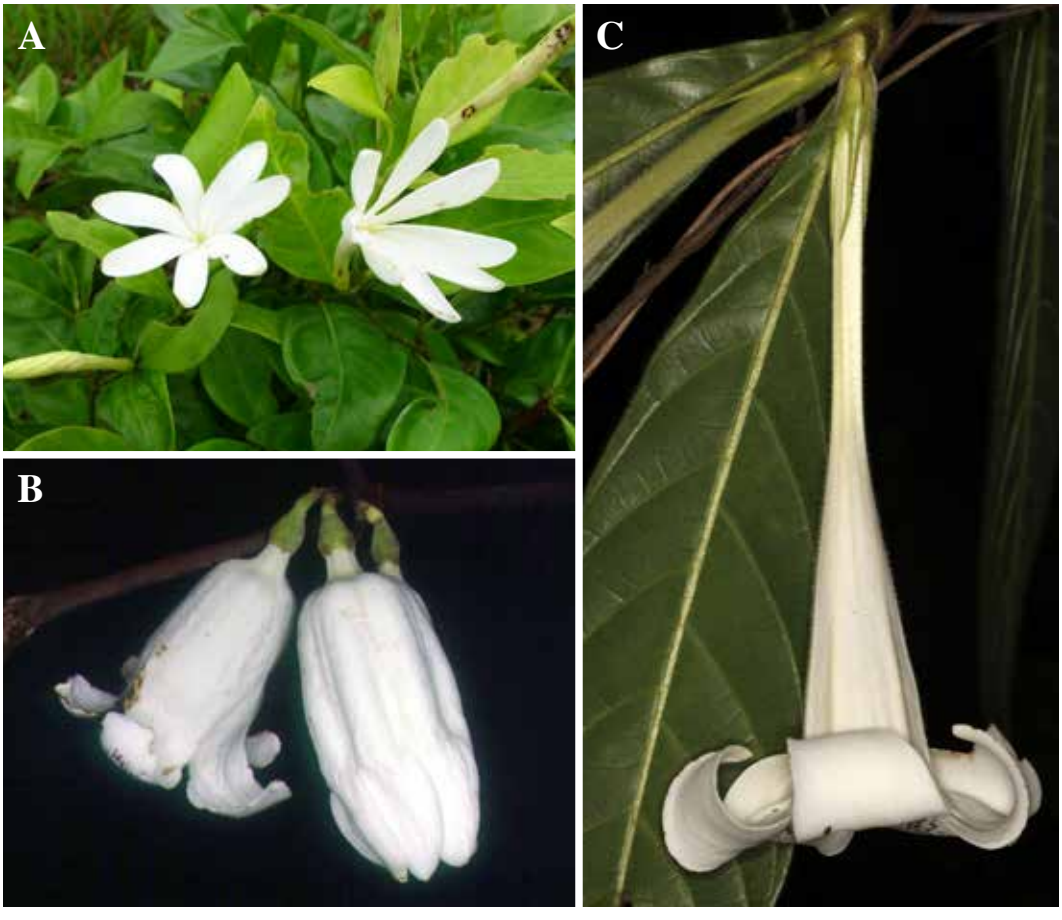

Fig. 6. Corolla forms of Asian taxa formerly placed in *Rothmannia*: hypocrateriform in *Ridsdalea merrillii* (**A**), campanulate in *Ridsdalea wittii* (**B**), and infundibular in *Singaporandia macrophylla* (**C**). Note corollas with more than five lobes in A. (Photos: A, R. Nilus; B, C. Puff; C, Ang Wee Foong)

occurs in Africa and is common among *Rothmannia* complex species there, e.g., *R. lujae*, *R. longiflora*, *R. fischeri* ssp. *verdcourtii* Bridson, and *R. whitfieldii*. However, in Malesia, it is only known in *Rothmannia macrophylla* (Fig. 6C). The other uncommon corolla form is here described as subhypocrateriform with long lobes. It is only found in the genus *Kochummenia* (Fig. 9).

Corolla lobe characters. The corolla lobes are contorted and overlap either to the right (only in Africa: *Rothmannia annae, R. capensis*, *R. fischeri*, *R. hispida, R. lateriflora* (K.Schum.) Keay, *R. liebrechtsiana* (De Wild. & T.Durand) Keay, *R. octomera* (Benth. & Hook.f.) Fagerl., *R. ravae* and *R. urcelliformis*) or left (all the rest of the complex in Africa, Asia

and SW Pacific; Fig. 6A–6C). According to Robbrecht (1988), species with contorted lobe aestivation usually have left-contorted lobes. In the *Rothmannia* complex, right-contorted corolla lobes seem to be confined to the nine African species mentioned earlier. This type has also been documented in *Hyperacanthus* E.Mey. ex Bridson and *Phellocalyx* of the Gardenieae (Robbrecht 1988). The corolla lobes for *Kochummenia* are contorted to the left.

Rothmannia complex species typically have five corolla lobes, but this may increase to 6–8, as in *R. merrillii* (Fig. 6A) and *R. negrosensis* (Merr.) J.T.Pereira & Ridsdale (Malesia), and *R. octomera* (Africa). The shape of the corolla lobes in the Malesian species is very variable: elliptic (narrowly to broadly), ovate, ovate-elliptic, or lanceolate. In *Kochummenia* the corollas are pentamerous and corolla lobe shape is linear. The corolla lobe apices in the African species with right-contorted corolla are always all acute or pointed, whereas species with left-contorted corolla have both pointed to obtuse corolla lobes. In the Asian and SW Pacific species of the *Rothmannia* complex, most have obtuse corolla lobe apices; only in *Kochummenia*, *Gardenia forsteniana* and *Rothmannia macrophylla* are they pointed.

Coloration. The outer part of the corolla tube can be white or creamy-white (e.g., the mainland Asian *Rothmannia wittii* and the Malesian *R. merrillii*) (Fig. 6A, B) to greenish (e.g., the African *R. annae*) in Asian, SW Pacific and some African taxa; or yellowish brown to brownish (e.g., the African *R. whitfieldii*, *R. munsae* (Schweinf. ex Hiem.) E.M.A.Petit subsp. *megalostigma* (Wernham) Somers); or suffused pink-crimson (e.g., *R. longiflora*) in some African taxa. In the Malesian *Rothmannia macrophylla*, the outer surface of the tube is white (Fig. 6C) or sometimes with a maroon tinge at the base.

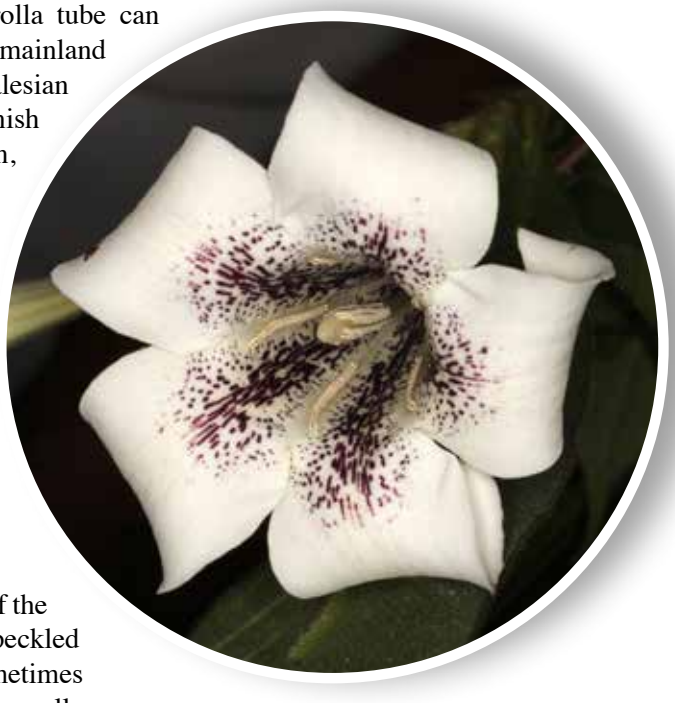

Fig. 7. Freshly opened flower of *Singaporandia macrophylla*, showing speckling of the inner tube surface and secondary pollen presentation (with pollen from early-dehiscent anthers deposited on the still-immature stigma just prior to floral opening). (Photo: Ang Wee Foong)

The corolla mouth and uppermost part of the corolla tube (corolla throat) may be speckled to non-speckled. These speckles can sometimes be seen on the base or central part of the corolla lobes. The majority of the African species have speckled corollas (in *Rothmannia lujae* speckling has not been documented but in *R. whitfieldii*, non-speckled corollas are typical). In mainland Asia (i.e., Thailand, Indo-China,

Myanmar, South China) and the Andaman Islands, the corollas are speckled. In Malesia, *Rothmannia schoemanii* and *R. macrophylla* (Fig. 7) have speckled corolla, the rest are without colouration (e.g., *R. merrillii*). The colour of the speckling may vary from pink (e.g., *Rothmannia annae* from Africa) to purple or reddish purple (e.g., the African *R. longiflora*, and the Asian *R. thailandica*, *R. wittii* and *R. macrophylla*) and rarely said to be "deep blue" (in *R. vietnamensis*, Tirvengadum 1982). The corolla throat is non-speckled in *Kochummenia*.

Corolla indumentum. The inner surface of the tube is glabrous in the Malesian *Gardenia forsteniana, G. pseudoternifolia*; *Kochumennia*; *Randia anisophylloides*, *Rothmannia graciliflora* (Merr.) J.T.Pereira & Ridsdale, *R. lagunensis, R. leytensis* J.T.Pereira & Ridsdale and *R. macromera*. In Malesia, corolla tube hairiness on the inside may be recognized as two types: with a hairy zone covering part or all of the tube from the mouth downwards in *Gardenia grandis, Rothmannia merrillii, R. negrosensis* and *Timonius nigrescens* Valeton, or with a hairy zone covering part or all of the tube below the level of the anthers in *R. schoemanii* and *R. macrophylla*. In Africa, the majority of species are with a hairy zone covering part or all of the tube below the level of the anthers downwards, e.g., *Rothmannia capensis*, *R. engleriana*, *R. ravae*, *R. longiflora*, *R. whitfieldii*, and *R. lujae*. A few African species (e.g., *Rothmannia globosa*, *R. hispida* (K.Schum.) Fagerl. and *R. manganjae*) have the hairy zone covering part or all of the corolla tube from the mouth downwards. *Rothmannia* complex species from mainland Asia (including the Andaman Islands) also have two types of hair distribution on the inner surface of the corolla tube. Most mainland Asian species have a hairy zone covering part of the tube below the level of the anthers, as in, e.g., *Rothmannia pulcherrima*, *R. venalis*, *R. sootepensis*, but a few species (e.g., *R. vidalii* and *R. wittii*) have a hairy zone covering part of the tube from the mouth downwards. None of the *Rothmannia* complex species in mainland Asia (including Andaman Islands) has a glabrous inner corolla tube surface.

The distribution of indumentum on the outer surface of the corolla lobes can be distinguished as three main types as follows:

(i) glabrous or with minute hairs sparsely distributed at the margin or fringes of the lobes (e.g., *Rothmannia annae, R. capensis, R. fischeri, R. lujae* and *R. ravae* (all African) and *R. lagunensis, R. merrillii, R. pulcherrima, R. sootepensis, R. thailandica, R. venalis,* and *R. vietnamensis*; all Asian and SW Pacific);

(ii) sparsely to densely hairy on the uncovered half of the corolla lobes (e.g., *Gardenia forsteniana, G. grandis, G. pseudoternifolia; Kochummenia*; *Randia anisophylloides*; *Rothmannia daweishanensis, R. eucodon, R. graciliflora, R. kampucheana, R. leytensis, R. macromera*, *R. macrophylla, R. negrosensis*, and *R. schoemanii*: all Asian and SW Pacific);

(iii) hairs uniformly covering the entire lobe outer surface (e.g., *Rothmannia wittii* and *R. vidalii* (Asian) and all the left-contorted African species (except *R. lujae*) and right-contorted African species (*R. hispida, R. lateriflora*, and *R. octomera*).

Placentation and ovules. The common placentation type in the Rubiaceae is axile (Puff 2001). Parietal placentation (2 parietal placentas opposite each other and sometimes partially fused) has been described for African species of the *Rothmannia* complex (Hallé 1970, Bridson & Verdcourt 1988, and Sonké & Simo 1996). We have verified parietal placentation in a few of the African species: *Rothmannia capensis, R. engleriana, R. fischeri* (ssp. *fischeri* and ssp. *verdcourtii*) and *R. manganjae*. However, our examination of two African species, *Rothmannia longiflora* and *R. whitfieldii* has revealed that placentation is in fact axile, and so is different from that recorded by others. Similarly, Tirvengadum (1982), who studied the South and Southeast Asian species, mentioned that the placentation is parietal with 2 placentas, the base of which sometimes forms an incomplete septum. However, we have found that most of the species studied by Tirvengadum (1982) (e.g., *Rothmannia eucodon, R. kampucheana, R. sootepensis, R. venalis*, *R. vietnamensis* and *R. wittii*) have axile placentation with complete septum development in the ovary. Shui et al. (2003), who described *Rothmannia daweishanensis* from South China, documented the seemingly 2-locular ovary as having a parietal placentation. In all the Malesian species (including *Rothmannia macrophylla*), the placentation is axile, as has been noted by Wong (1984, 1989). Our investigation of this character for most of the African and some of the mainland Asian species was not possible because of insufficient flowering material. Nevertheless, based on present studies, both parietal and axile placentations exist within the *Rothmannia* complex. In *Kochummenia* spp., the placentation is axile, as noted by Wong (1989).

In all the *Rothmannia* species, the number of ovules is numerous, as mentioned by Tirvengadum (1982), Robbrecht & Puff (1986), Bridson & Verdcourt (1988), Sonké & Simo (1996), and Puff et al. (2005). This is also true for the species of *Kochummenia*.

Stamens. The anthers in all *Rothmannia* s.l. species are (dorsi-)medifixed, sessile or subsessile and linear in shape. There are typically 5, rarely 6, anthers but in a few species this may increase in number, e.g., *Rothmannia merrillii* (6–10), *R. negrosensis* and *R. octomera* (6–8). The anthers in all the *Rothmannia* complex species are attached above the basal 1/3 of the corolla tube and they may be fully included within the tube (or sometimes the anther tips slightly protrude from the corolla tube) or partially exsert. In the Malesian species (including *Rothmannia macrophylla*), all the anthers are typically included within the tube (above the basal 1/3 of the corolla tube) but sometimes the tips of anthers may protrude slightly, e.g., in *R. lagunensis*, *R. leytensis, R. macrophylla* and *R. schoemanii*. Included anthers were also documented in some of the African species, e.g., *Rothmannia globosa*, *R. longiflora*, *R. manganjae* and *R. whitfieldii* (Bridson & Verdcourt 1988) and some of the mainland Asian species (e.g., *R. eucodon, R. pulcherrima, R. vidalii* and *R. wittii*). In the majority of the African species (e.g., *Rothmannia annae*, *R. capensis* and *R. ravae*) and mainland Asian species (e.g., *R. kampucheana*, *R. sootepensis, R. thailandica, R. venalis* and *R. vietnamensis*), the anthers are partially exsert; this is not found in the Malesian species. The anther length in the Malesian species typically range from 5 mm to 15 mm long; however, the longest, 20–25 mm, is found in *Rothmannia macrophylla*. The extremely long anthers

of *Rothmannia macrophylla* distinguished this taxon from the rest of the Malesian species. Many of the African species have longer anthers, more than 20 mm long, and may reach up to 60 mm long (e.g., in *Rothmannia macrocarpa* (Hiern) Keay, Hallé 1970).

In *Kochummenia,* the anthers are also (dorsi-)medifixed, sessile or on short filaments, and linear in shape. There are 5 included anthers, 10–12 mm long, attached at the lower 1/3 of the corolla tube; the low insertion of the anthers within the corolla tube differentiates *Kochummenia* from the rest of the *Rothmannia* complex.

Secondary pollen presentation and pollen characteristics

Secondary pollen presentation (SPP) is the condition when pollen is shed onto the outside of the immature style-stigma complex, sometimes also just referred to as the "stylar head" (Robbrecht & Puff 1986). As the flower matures, the style elongates and the stylar head or stigma comes into proximity with the anthers, which dehisce just before floral opening, depositing the pollen onto the still-immature stigma. When the flower opens, the stylar head acts as a "pollen presenter". Only subsequently does the stigma become receptive. Although this is a frequent phenomenon in the Gardenieae, our observations do not show a consistent presence of SPP in all species of the *Rothmannia* complex. Fresh flowering material of three Malesian species (i.e., *Gardenia pseudoternifolia*, *Rothmannia merrillii* and *R. schoemanii*) were investigated for the occurrence of SPP.

In both *Gardenia pseudoternifolia* and *Rothmannia merrillii*, dissected buds of advanced development revealed that the pollen sacs were still intact (without signs of dehiscence) although the style and stigma were located only up to 2/3 the length of the corolla tube and much below the anthers; furthermore, the stigmatic lobes were already parted (indicating female receptivity). In these species, SPP does not seem to be present, although the occurrence of heterostyly was not ascertained. On the other hand, in *Rothmannia schoemannii* (Fig. 8), buds of advanced development had the already-dehisced anthers appressed to the stigma, with pollen deposition on the style-stigma complex, so that it can be concluded that SPP definitely occurs. Examination of herbarium material of

Fig. 8. *Ridsdalea schoemanii*, longitudinal section through floral buds just prior to floral opening, with pollen already shed from dehisced anthers and deposited onto the stigma, which acts as a pollen presenter as the flower opens. (Photo: E.M. Lai)

several other Malesian species of the *Rothmannia* complex, e.g., *Gardenia forsteniana, G. grandis*, *Randia macromera* var. *uvarioides* Valeton, *Rothmannia lagunensis, R. leytensis, R. macromera*, and also one African species, *R. lujae,* also indicated the likely occurrence of SPP. In some cases, the stigmatic lobes had grooves (in *Randia macromera var. uvarioides* and *Rothmannia macromera*) and hairs (in *Randia macromera* var. *uvarioides*), which according to Robbrecht & Puff (1986) assisted pollen deposition. SPP is also present in *Rothmannia macrophylla* (Fig. 7), but there are no observations for *Kochummenia*.

Pollen of the following species of the *Rothmannia* complex in Asia were also studied by one of us (Pereira 2008): *Gardenia forsteniana*, *G. grandis*, *G. pseudoternifolia*; *Randia anisophylloides*; *Rothmannia graciliflora, R. kampucheana, R. leytensis*, *R. macromera*, *R. merrillii*, *R. negrosensis*, *R. pulcherrima*, *R. schoemanii*, *R. sootepensis*, *R. venalis*, *R. vidalii*, *R. vietnamensis*, *R. wittii*; *Timonius nigrescens*, and several unnamed species. Prior to this study, only a small number of the *Rothmannia* complex members have been palynologically studied (*Rothmannia capensis, R. engleriana, R. longiflora* and *R. globosa* (African) by Persson (1993) and *R. fischeri* (African) by Verdcourt (1958); *R. macrophylla* (Sharma 1968), *R. schoemanii* (Sharma 1968, Mitra 1969), *R. sootepensis* (Sharma 1968, Persson 1993) and *Randia* (= *Kochummenia*) *stenopetala* (Asian) by Sharma (1968) and Persson (1993). The findings of these previous investigations have conformity as well as contradiction with the results we have obtained. The detailed pollen characteristics, as compared with *Kochummenia parviflora*, *K. stenopetala* and *Rothmannia macrophylla*, will be reported in a separate contribution, and only the most consistent differences for the groups are mentioned here.

Although only four species of the African type alliance (*Rothmannia* s.s.) were surveyed for the pollen studies, the results were consistent in that their pollen have luminal processess that are not present in the rest of the other *Rothmannia* species or *Kochummenia*. Igersheim (1991) commented that the occurrence of luminal processes is uncommon in the Rubiaceae and is known in only a limited number of groups, e.g., *Paederia* subgenus *Lecontea* and several genera in the *Morindeae* (Johansson 1987).

The main diagnostic characters differentiating *Rothmannia macrophylla* from the rest of the Asian *Rothmannia* complex and *Kochummenia* lie in the very wide ectocolpus (7.1–11.8 μm) and large average pollen size (polar axis P=34 μm, equatorial diameter E=35.9 μm), compared to the other species of *Rothmannia* and *Kochummenia* (ectocolpus width only up to 5 μm wide and moderate pollen size with P=26.5 μm, E=32.3 μm). The reticulate to microreticulate sexine ornamentation in *Kochummenia* is quite similar to that in other taxa of the *Rothmannia* complex including *R. macrophylla*; however, the difference is in the ectoaperture. In *Kochummenia,* the ectoaperture margin is vague and the length is only up to 1/2 the grain margin-pole distance in polar view, whereas in the other *Rothmannia* complex taxa including *Rothmannia macrophylla*, the ectocolpus margin is always distinct and the length reaches 3/4 of the grain margin-pole distance in polar view.

SYSTEMATIC PART:
MORPHOLOGICAL DISTINCTION OF THREE ASIATIC GENERA

For the Asiatic allies of the *Rothmannia* complex, our analyses have revealed three major groupings that could be recognized as distinct genera. Each has at least two unique characteristics among the complex in Asia, and confirmed or possibly unique differences from their African allies (these having been shown to belong to a completely different genetic clade or alliance) and incomplete surveys of other character-states indicate there could be more differences found as study opportunities increase in the future.

Kochummenia is distinct by its subhypocrateriform corolla with linear lobes exceeding the tube (Fig. 9) and anthers inserted near the tube base (and likely also leaf epidermal cells with deeply sinuated anticlinal walls). The first two are unique character states defining a genus so far known only from the Malay Peninsula (as far as we know, only within Peninsular Malaysia). *Ridsdalea* J.T.Pereira & K.M.Wong, one of the two new genera recognized here, is characterized by a hypocrateriform or campanulate corolla (Fig. 6A, B; Fig. 10) and reduction of only one member of the distal leaf pair on each branch segment that results in a trifoliate leaf cluster formed with the proximal leaf pair (Fig. 1: A2; Fig. 3, 4, 11). *Ridsdalea* is the most widespread of the three, occurring across subtropical and tropical Asia to Malesia.

Fig. 9. Inflorescences of *Kochummenia stenopetala*. (Photo: Ahmad Fitri Zohari)

The other new genus, *Singaporandia* K.M.Wong, is based on *Rothmannia macrophylla*, and is distinguished by an infundibular corolla (Fig. 6C), exceptionally long anthers with large pollen and ectocolpus, and a distinctive plant architectural form characterized by complete reduction of the second (distal) leaf pair on a branch segment (Fig. 1: B2, 5). This monotypic genus is distributed in the Malay Peninsula (Peninsular Malaysia and Singapore) and Sumatra.

Kochummenia K.M.Wong

Malay. Nat. J. 38 (1984) 31; Wong, Tree Fl. Malaya (1989) 366. TYPE SPECIES: *Kochummenia stenopetala* (King & Gamble) K.M.Wong.

Gardenia sensu King & Gamble, J. As. Soc. Beng. 72 (1903) 218, pro parte quoad *Gardenia stenopetala* King & Gamble.

Randia sect. *Grandiflorae* Ridl., Fl. Malay Penins. 2 (1923) 71, pro parte quoad *R. stenopetala* Ridl.

Rothmannia sensu Bremek., pro parte, Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs., quoad *Rothmannia stenopetala* (Rild.) Bremek. (*sic!*).

Shrubs or treelets with typically solitary trunk; unarmed. ***Trunk*** orthotropic with continuous production of branches. ***Branches*** opposite and decussate on the trunk, plagiotropic by substitution, sympodial in development; primary branch and successive higher-order modular branch units each with only 2 nodes and a terminal inflorescence each, new modular units developing from either or both leaf axils at the proximal node of the previous module. ***Stipules*** interpetiolar, free, persistent, inner surface hairy with 2–3 rows of colleters at the basal part. ***Leaves*** typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves; petiolate to subsessile, axils of the midrib and lateral veins frequently with domatia on the lower leaf surface, margin entire. ***Inflorescences*** terminal in origin but later appearing lateral because of displacement to one side during sympodial branch development; distinctly pedunculate to subsessile, distinctly branched cymes. ***Flowers*** bisexual; small or medium, corolla tube typically not more than 3 cm long; typically pedicellate, sometimes subsessile. Calyx 5-lobed, colleters present in small groups on the inner surface, hairy on the outside. Corolla 5-merous; subhypocrateriform; the tube creamy-white to greenish, the lobes creamy-white to greenish; the outer surface glabrous or hairy, the inner surface glabrous; lobes contorted to the left in the flower bud, distinctly longer than the tube; stamens dorsifixed, attached at the lower part of the corolla tube, fully included within the tube, anthers sessile or on short filaments, linear; style shorter than the corolla tube, glabrous; stigma included, narrowly subovoid, 2-lobed, smooth when dried;

ovary 2-celled; ovules many, placentation axile. Mature ***fruits*** berry-like, medium, to 3.5 cm across; ellipsoid, crowned with persistent calyx, outer surface glabrescent to sparsely hairy, drying smooth or wrinkled; 2-loculate. ***Seeds*** many, immersed in a pulp-like placental tissue.

DISTRIBUTION. Three species, endemic to the Malay Peninsula (so far known only in Peninsular Malaysia).

NOTES. The genus is named after K.M. Kochummen (1931–1999), Malaysian botanist based at the Forest Research Institute Malaysia. The type species, *Randia stenopetala* Ridl., was placed under *Randia* sect. *Grandiflorae* by Ridley (1923), who considered it closely related to *Randia macrophylla* (= *Singaporandia macrophylla* in the present account).

1. *Kochummenia parviflora* K.M.Wong

Malay Nat. J. 38 (1984) 32; Wong, Tree Fl. Malaya (1989) 366. TYPE: *Sinclair & Kiah SFN 39935*, Peninsular Malaysia, Terengganu, 36th mile Terengganu-Besut road, 13 Jul 1953 (holotype SING; isotypes K, L).

DISTRIBUTION. Thus far endemic to Terengganu state, Peninsular Malaysia. Only known from a few collections (Wong 1984).

2. *Kochummenia stenopetala* (King & Gamble) K.M.Wong

Malay. Nat. J. 38 (1984) 32; Wong, Tree Fl. Malaya (1989) 366. Basionym: *Gardenia stenopetala* King & Gamble, J. As. Soc. Beng. 72 (1903) 218. *Randia stenopetala* (King & Gamble) Ridl., Fl. Malay Penins. 2 (1923) 79; Corner, Wayside Trees Malaya 1 (1952) 557. *Rothmannia stenopetala* (Ridl.) Bremek. (*sic!*), Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs. [First-step] LECTOTYPE (designated by Wong 1984): *Curtis 3144*, Perak, Bujong Malacca, Dec 1895 (SING) (isolectotype CAL). [Second-step] LECTOTYPE (designated here): *Curtis 3144*, Perak, Bujong Malacca, Dec 1895 (SING: barcode SING 0059292) (isolectotypes CAL, SING: barcode SING 0059294).

(Fig. 9)

DISTRIBUTION. So far endemic to Perak state, Peninsular Malaysia. Most of the collections were from the early to mid-20th century. Only recently recollected from Bujang Melaka and the Kledang Saiong Forest Reserve, Perak.

3. *Kochummenia* terengganuensis K.M.Wong, **sp. nov.**

This new species is closely related to *K. parviflora* K.M.Wong in having shorter corolla lobes than *K. stenopetala* (King & Gamble) K.M.Wong, but differs in the shorter (less than

1 cm long), hispid inflorescence rachis and hispid lower leaf surface (in *K. parviflora*, the inflorescence rachis is 1–2 cm long and, like the lower leaf surface, is sparsely pubescent).

TYPE: *Whitmore FRI 20362*, Terengganu, Kemaman Hills, 3 miles SW of Kg Ayer Putih, near Sg Buaya, 20 Aug 1971 (holotype KEP; isotypes SAR, SING).

Kochummenia sp.,Wong, Tree Fl. Malaya (1989) 366.

Treelet, to 1.5 m high. Twigs hispid. ***Stipules*** triangular, 4–6 mm long, 3.5–4 mm wide, hispid outside; apex long-acuminate, 2.5–3 mm long. Young ***leaves*** on shoot tips hispid on both sides. Mature leaves with petiole to 1 cm long, 1.5–2 mm thick, hispid; lamina narrowly elliptic, 20–30 cm long, 4–7 cm wide, upper and lower surfaces hispid, leaf base cuneate to sometimes unequal; leaf apex acute to acuminate, acumen to 1 cm long; chartaceous when dry; midrib on upper side flat to slightly raised, hispid, on lower side distinctly raised, hispid; secondary veins 10–13 pairs, on upper side flat, hispid, on lower side raised, hispid; tertiary venation visible as a much-branched network between pairs of secondary veins. ***Inflorescence (bud)***: peduncle to 0.2 cm long, *c*. 3 mm thick, hispid; habit compact, with *c*. 2 distinct branching orders, rachis 0.2 cm long, primary branches along rachis 1–2 pairs, *c*. 0.3 cm long; bracts narrowly ovate, *c*. 3 mm long, 2.5–3 mm wide, hispid. Flowers 6 per cyme; pedicels very short, *c*. 2 mm long, *c*. 1 mm thick; calyx tube 4–6 mm long, 2.5–3 mm wide, hispid, hairs erect, surface visible; calyx limb cup-shaped; calyx lobes 5, long-linear, 9–10 mm long, hispid; corolla subhypocrateriform, greenish white, the tube *c*. 0.6 cm long; non- speckled inside, outer surface pubescent to hispid, inner surface glabrous; corolla lobes 5, linear, 1.8–2.4 cm long, *c*. 0.1 cm wide, outside hispid on the half uncovered in the bud, inside glabrous. ***Fruits*** not seen.

DISTRIBUTION. Thus far, endemic to Terengganu state, Peninsular Malaysia. Known only from the type collection. Recorded in logged kapur forest, on shale.

Ridsdalea J.T.Pereira & K.M.Wong, **genus novum**

The new genus *Ridsdalea* is distinguished from *Rothmannia* Thunb. by its corolla lobes contorted to the left (the lobes in *Rothmannia* s.s. are contorted to the right), and from other related genera in the Asiatic *Rothmannia* alliance by its hypocrateriform or campanulate corolla (contrasting with the subhypocrateriform corolla with long linear lobes of *Kochummenia* K.M.Wong, and the infundibular corolla of *Singaporandia* K.M.Wong); and reduction of only one member of the distal leaf pair on each 2-node branch module resulting in a trifoliate leaf cluster formed with the proximal leaf pair (contrasting with *Singaporandia*).

TYPE SPECIES: *Ridsdalea grandis* (Korth.) J.T.Pereira

Gardenia sensu Linn., sensu Miq., Fl. Ind. Bat. 2 (1856) 228, pro parte quoad *G. grandis* Korth. & *G. schoemanii* Teijsm. & Binn.; sensu Merrill, J. Str. Br. Roy. As. Soc. Spec. No. (1921) 564 & sensu Masamune, En. Phan. Born. (1942) 682, pro parte quoad *G. grandis* Korth. & *G. merrillii* Elmer.

Randia sect. *Gardenioides* Hook.f., Fl. Brit. India 3 (1880) 114, pro parte quoad *R. exaltata* Griff.; Ridley, Fl. Malay Penins. 2 (1923) 71.

Randia sensu Koord. & Valeton, Bijdr. 8 (1902) 88 & sensu King & Gamble, J. As. Soc. Beng. 72 (1903) 214–215, pro parte quoad *R. exaltata*; sensu Merrill, J. Str. Br. Roy. As. Soc. Spec. No. (1921) 562–564, pro parte quoad *R. grandis* (Korth.) Valeton ex Winkler & *R. kuchingensis* W.W. Sm.; sensu Masamune, En. Phan. Born. (1942) 708, pro parte quoad *R. grandis* (Korth.) Valeton ex Winkler, *R. keithii* C.E.C.Fischer & *R. kuchingensis* W.W.Sm.; sensu Backer & Bakhuizen, Fl. Java 2 (1965) 310, pro parte quoad *R. schoemanii* (Teijsm. & Binn.) Bakh.f.

Rothmannia pro parte sensu Bremekamp, Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 3; Backer & Bakhuizen, Fl. Java 2 (1965); Tirvengadum, Nord. J. Bot. 3 (1983) 466; Wong, Malay. Nat. J. 38 (1984) 46; Wong, Tree Fl. Malaya (1989) 324; Puff & Wong, Sandakania 2 (1993) 13; Beaman & Anderson, Pl. Mt. Kinabalu 5 (2004) 340.

Treelets to small, medium or large trees with typically solitary trunk, unarmed. ***Trunk*** or above ground shoot an orthotropic system with continuous production of branches. ***Branches*** opposite and decussate on the trunk, typically plagiotropic by substitution, sympodial in development; primary branch (and successive higher-order modular branch units) with only 2 nodes and a terminal inflorescence each; higher-order modular units developing from either one or both leaf axils at the proximal node of the previous module. ***Stipules*** interpetiolar, free or only very slightly fused at the base, persistent to caducous, inner surface hairy with colleters restricted to 1–several rows at the basal part or forming a central triangular area. ***Leaves*** typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size) and the proximal node with a pair of normal leaves; petiolate to subsessile, axils of the midrib, secondary veins, and sometimes other vein junctions frequently with domatia on the lower leaf surface; margin entire. ***Inflorescences*** terminal in origin, later appearing lateral because of displacement to one side during sympodial branch development; distinctly cymose or sometimes much reduced to a 1-flowered structure (but always with bracts marking potential branching on the main inflorescence axis); distinctly pedunculate to subsessile. ***Flowers*** bisexual; small or large, corolla tube typically not more than 15 cm long; typically pedicellate, sometimes subsessile. Calyx 5–8(–10)-lobed, colleters present in small groups on the inner surface, glabrous or glabrescent to hairy on the outside. Corolla typically 5-merous (in Malesia, 2 species, *R. merrillii* and *R. negrosensis*, often 6–8); hypocrateriform, or campanulate (e.g., *R. forsteniana* and *R. schoemanii*); the tube creamy-white, the lobes creamy-white, in some

species (e.g., *R. schoemanii*) with purple or reddish purple speckles or blotches running down the corolla throat; the outer surface glabrous or hairy, the inner surface glabrous or with hairs covering part or all of the tube from either the corolla mouth downwards (*R. grandis, R. merrillii, R. negrosensis*, *R. nigrescens*) or below the level of the anthers (*R. schoemanii*); lobes contorted to the left in the flower bud, distinctly shorter than or more-or-less as long as the tube; stamens (dorsi-)medifixed, attached at the upper part of the corolla tube or sometimes the tips slightly protruding (inserted above the basal 1/3), anthers sessile or on short filaments, linear; style shorter than, as long as, or slightly exceeding the corolla tube, or (rarely) of two lengths in a heterostylous condition, mostly glabrous, but sometimes (e.g., *R. schoemanii*) with scattered hairs; stigma included or (rarely) partially exsert, clavate to fusiform and sometimes narrowly oblong, 2-lobed, smooth to ribbed or grooved when dried; ovary 2-celled; ovules many, placentation axile. Mature ***fruits*** berry-like, indehiscent, medium to large, 2–5 cm or more across; globose or sub-globose or broad ellipsoid, outer surface drying smooth; 2-loculate. ***Seeds*** many, immersed in a pulp-like placental tissue.

DISTRIBUTION. *Ridsdalea* is widespread, through mainland Asia and the Malay Peninsula into East Malesia.

NOTES. There are c. 30 species in this genus, which is named after Colin E. Ridsdale (b. 1944), Rubiaceae specialist based in the Netherlands. The necessary combinations for 25 published names are effected here, with their synonyms where applicable. Full species descriptions and new species will be included in a forthcoming revision of the Malesian species.

1. *Ridsdalea anisophylloides* (Wernham) J.T.Pereira, **comb. nov.**

Basionym: *Randia anisophylloides* Wernham, J. Bot. 56 (1918) 74. TYPE: *Forbes 626*, Papua New Guinea, Central Prov., Sogere region, Mt Korroro, 2000 ft [609 m] alt, 29 Jan 1886 (holotype BM; isotype P).

DISTRIBUTION. Thus far known from the Windowoi Mountain in West Irian Jaya Province, Indonesia, and Papua New Guinea (Central, Madang, Northern, and East Sepik Provinces).

2. *Ridsdalea attopevensis* (Pit.) J.T.Pereira, **comb. nov.**

Basionym: *Randia attopevensis* Pit., Fl. Gén. Indo-Chine 3 (1923) 246. *Rothmannia attopevensis* (Pit.) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs. LECTOTYPE (here designated): *Harmand per Pierre 6206*, Laos, Attopeu (P: accession MNHN-P-P00196978) (isolectotype P: accession MNHN-P-P00196979).

DISTRIBUTION. Vietnam and Laos.

3. *Ridsdalea daweishanensis* (Y.M.Shui & W.H.Chen) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia daweishanensis* Y.M.Shui & W.H.Chen, Novon 13 (2003) 322; Zhang et al., Acta Phytotax. Sin. 45(1) (2007) 92. TYPE: *Shui et al. 14496*, China, Yunnan, Maguan, Gulinqing, Woody Station nearby Nanxi Community of Hekou (holotype KUN; isotypes KUN, MO).

DISTRIBUTION. SW China (Yunnan province), Vietnam.

4. *Ridsdalea eucodon* (K.Schum.) J.T.Pereira, **comb. nov.**

Basionym: *Randia eucodon* K.Schum. in Schmidt, Fl. Koh Chang (1902) 183. *Rothmannia eucodon* (K.Schum.) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7, in obs. TYPE: *Schmidt 717*, Thailand, Koh Chang 717 (holotype C; isotype K).

Randia exaltata var. *griffithiana* Pierre ex Pit., Fl. Gén. Indo-Chine 3 (1923) 245. LECTOTYPE (here designated): *Pierre 1625*, Vietnam, Bienhoa, Bao Chiang (P: barcode P00199261) (isolectotypes K, NY, P: barcode P00199260).

DISTRIBUTION. Thailand and Vietnam.

5. *Ridsdalea forsteniana* (Miq.) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia forsteniana* Miq., Ann. Mus. Bot. Lugduno-Batavi 4 (1869) 236; Koorders, Meded. 's Lands Plantentuin 19 (1898) 494; Koords.-Schum., Syst. Verz. 11 (1914) 121; Koorders, Suppl. Fl. N.O. Celebes Part II (1922) 59, pl. 125. LECTOTYPE (here designated): *Forsten 386*, Celebes, Amurang, Nov 1860 (L: sheet n. 908.216-335).

Gardenia pelenkahuana Teijsm. & Binn. ex Koord., Meded. 's Lands Plantentuin 19 (1898) 495. LECTOTYPE (here designated): *Koorders Kds. 19707β*, Celebes, Minahasa, 20 Mar 1895 (BO).

Rothmannia forsteniana Miq., nom. invalid., Kessler et al., Checkl. Woody Plants Sulawesi, Blumea Supp. 14 (2002) 121.

DISTRIBUTION. Confined to Sulawesi (North, Central, Gorontalo and South Provinces).

6. *Ridsdalea graciliflora* (Merr.) J.T.Pereira, **comb. nov.**

Basionym: *Randia graciliflora* Merr., Philipp. J. Sci., C 10 (1915) 109; Merrill, Enum. Philip. Fl. Pl. 3 (1923) 527. *Rothmannia graciliflora* (Merr.) J.T.Pereira & Ridsdale, Sandakania 18

(2012) 17. LECTOTYPE (designated by Pereira & Ridsdale 2012): *Miranda F.B. 17988*, Philippines, Mindanao, Misamis, Mt Malindang, Jan–Feb 1913 (US) (isolectotypes K, L, NY, P, SING).

Gardenia negrosensis sensu Merrill, Philip. Fl. Pl. 3 (1923) 527 pro parte quoad *Ramos & Edaño B.S. 36787*; non Merrill (1915).

DISTRIBUTION. Southern Philippines (Mindanao and Basilan).

7. *Ridsdalea grandis* (Korth.) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia grandis* Korth., Ned. Kruidk. Arch. 2 (1851) 191; Walp., Ann. Bot. Syst. 2 (1851) 796; Miq., Fl. Ind. Bat. 2 (1856) 231; Miq., Ann. Mus. Bot. Lugduno-Batavi 4 (1869) 236; Merrill, Bibl. En. Born. Pl., J. Straits Branch Roy. Asiat. Soc., Sp. No. (1921) 564; Masamune, En. Phan. Born. (1942) 708. *Randia grandis* (Korth.) Valeton ex Winkler, Bot. Jahrb. Syst. 44 (1910) 559; Merrill, Bibl. En. Born. Pl., J. Straits Branch Roy. Asiat. Soc., Sp. No. (1921) 562; Masamune, En. Phan. Born. (1942) 708; Coode et al., Checkl. Flow. Pl. & Gymn. Brunei (1996) 289. TYPE: *Korthals s.n.*, Borneo, Kalimantan, Mt Sakoembang, sine datum (holotype L: sheet no. 908.216-321).

Randia kuchingensis W.W. Smith, Notes Roy. Bot. Gard. Edinb. 8 (1915) 326; Merrill, Bibl. En. Born. Pl., J. Straits Branch Roy. Asiat. Soc., Sp. No. (1921) 562; Masamune, En. Phan. Born. (1942) 708. *Rothmannia kuchingensis* (W.W. Smith) K.M.Wong, Malay. Nat. J. 41 (1987) 270, Tree Fl. Malaya 4 (1989) 406. LECTOTYPE (designated by Wong et al., 1987): *Haviland 676*, Sarawak, Kuching, 29 Dec 1892 (SING) (isolectotypes BM, L).

Rothmannia malayana K.M.Wong, Malay. Nat. J. 38 (1984) 51, Tree Fl. Malaya 4 (1989) 406. TYPE: *Loh FRI 19252*, Kelantan, proposed Batu Papan F.R., 22 Feb 1972 (holotype KEP; isotypes K, SING).

DISTRIBUTION. Peninsular Malaysia (Kelantan, Pahang and Johor states), Sumatera (West, South and Riau Provinces) and Borneo (Kalimantan, Sarawak and Brunei).

8. *Ridsdalea kampucheana* (Tirveng.) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia kampucheana* Tirveng., Nord. J. Bot. 3(4) (1983) 466. TYPE: *Poilane 14676*, Cambodia, nord de Kampot, 5 Feb 1928 (holotype P).

DISTRIBUTION. Cambodia.

9. *Ridsdalea lagunensis* (Merr.) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia lagunensis* Merr., Philip. J. Sci., C 10 (1915) 110; Enum. Philip. Fl. Pl. 3 (1923) 530. *Rothmannia lagunensis* (Merr.) J.T.Pereira & Ridsdale, Sandakania 18 (2012) 18. NEOTYPE (designated by Pereira & Ridsdale 2012): *Ramos Bur. Sci. 14934*, Philippines, Luzon, San Antonio Province, Laguna, Jun 1912 (L) (isoneotype P).

DISTRIBUTION. Known only from Luzon island of the Philippines

10. *Ridsdalea leytensis* (J.T.Pereira & Ridsdale) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia leytensis* J.T.Pereira & Ridsdale, Sandakania 18 (2012) 27. TYPE: *Wenzel 641*, Philippines, Leyte, 8 Mar 1914 (holotype A; isotype BM).

Gardenia negrosensis sensu Merrill, Enum. Philip. Fl. Pl. 3 (1923) 530, pro parte quoad *Wenzel 741, 641*; *Sandique 26596*; non Merrill (1915).

DISTRIBUTION. Endemic to the Philippines (Leyte).

11. *Ridsdalea macromera* (Lauterb. & K.Schum.) J.T.Pereira, **comb. nov.**

Basionym: *Randia macromera* Lauterb. & K.Schum., Fl. Deutsch. Schutzgeb. Südsee (1900) 562; Valeton, Bot. Jahrb. Syst. 60 (1926) 90 excl. var. *uvarioides* Valeton (= *Ridsdalea uvarioides*); Merrill & Perry, J. Arnold Arbor. 25 (1944) 202. *Rothmannia macromera* (Lauterb. & K.Schum.) Fagerl., Ark. Bot. 30 A (7) (1943) 39. NEOTYPE (here designated): *Schlechter 16215*, Papua New Guinea, Kaiser Wilhelmsland, 29 Jun 1907 (L: sheet no. 927.320-165).

NOTES. In the original publication of the basionym, *Randia macromera* in the Fl. Deutsch. Schutzgeb. Südsee (1900), Lauterbach and Schumann cited two specimens, *Lauterbach 1286* (flowering) and *Lauterbach 1524* (flowering and fruiting), both from *Kaiser Wilhelmsland* (formerly the German colony of the northeastern part of mainland New Guinea), and collected in 1890. Both these specimens (together with their duplicates) were not located. According to Van Steenis-Kruseman (1950) in *Cyclopaedia of Collectors* Vol. 1, collections from Lauterbach's trip to *Kaiser Wilhelmsland* in 1890 were deposited in the Berlin Herbarium. There is a possibility that these specimens were destroyed during the Second World War. Attempts were made to locate the syntypes in the Berlin Herbarium and other herbaria where Lauterbach's collection were believed to have been deposited, i.e., BO, BM, K, L, and the US (Van Steenis-Kruseman 1950). However, the search was futile.

A later publication by Valeton (1926), *Die Rubiaceae von Papuasien*, listed again two of the specimens (i.e., *Lauterbach 1286* and *Lauterbach 1524*) cited by Lauterbach & Schumann (1900) and three other collections under *Randia macromera*. One of the specimens cited in this account was *Schlechter 16215*, collected on 29 June 1907 from Kaiser Wilhelmsland, found at L. This is the only specimen possible to find and which also matches the original description. As such, the specimen at Leiden (Herb. Ludg. Bat. accession no. 927.320-165) is designated as the neotype for this species.

DISTRIBUTION. Found so far only in Papua New Guinea (Morobe Province).

12. *Ridsdalea merrillii* (Elmer) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia merrillii* Elmer, Leafl. Philipp. Bot. 1 (1906) 5; Leafl. Philipp. Bot. 4 (1912) 1330; Gibbs, Journ. Linn. Soc. Bot. 42 (1914) 94; Merr., Enum. Philip. Fl. Pl. 3 (1923) 530; Merr., Philipp. J. Sci. 29 (1926) 421, pro parte excl. Celebes specimens; Merr., Bibl. En. Born. Pl., J. Straits Branch Roy. Asiat. Soc., Sp. No. (1921) 564 pro parte quoad *Gibbs 4340*, *Foxworthy 600*; Masamune, En. Phan. Born. (1942) 682. *Rothmannia merrillii* (Elmer) J.T.Pereira & Ridsdale, Sandakania 18 (2012) 20. LECTOTYPE (designated by Pereira & Ridsdale 2012): *Merrill 669*, Philippines, Island of Calomian, Culion, Feb 1903 (US) (isolectotypes A, K, NY, SING: barcode SING0093444).

Randia keithii C.E.C.Fisch., Bull. Misc. Inform. Kew (1932) 180; Masamune, En. Phan. Born. (1942) 708. *Rothmannia keithii* (C.E.C.Fisch.) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs. TYPE: *Keith 1215*, North Borneo, Sandakan, 500 ft [152 m] alt, 20 Feb 1929 (holotype K). (Fig. 6A)

DISTRIBUTION. Endemic to the Philippines and Borneo (Sabah).

13. *Ridsdalea negrosensis* (Merr.) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia negrosensis* Merr., Philipp. J. Sci., C 10 (1915) 111–112, pro parte quoad *Celestino Bur. Sci. 7333*, Merr., Enum. Philip. Fl. Pl. 3 (1923) 530, pro parte quoad *Ramos & Edaño Bur. Sci. 31358* & *Cardona FB 23868*, excl. *Ramos & Edaño Bur. Sci. 36787* (= "*Rothmannia graciliflora*"), *Sandique FB 26596*, *Wenzel 641* (= "*R. leytensis*"). *Rothmannia negrosensis* J.T.Pereira & Ridsdale, Sandakania 18 (2012) 25. LECTOTYPE (designated by Pereira & Ridsdale 2012): *Celestino Bur. Sci. 7333*, Philippines Negros, Cadiz, Feb–Mar 1909 (L).

DISTRIBUTION. Thus far only found in the Philippines (Negros, Mindoro and Palawan islands).

14. *Ridsdalea nigrescens* (Valeton) J.T.Pereira, **comb. nov.**

Basionym: *Timonius nigrescens* Valeton, Engl. Bot. Jahrb. Syst. 61 (1927) 46. LECTOTYPE (here designated): *Ledermann 9560*, New Guinea, Sepik, 1912–13 (L) (isolectotype A).

Randia bartlettiana Merr. & Perry, J. Arnold Arbor. 29 (1948) 165. TYPE: *Clemens 41856*, Papua New Guinea, Morobe district, Boana, 2500–4500 ft [762–1371 m] alt, 26 Sep 1940 (holotype A; isotypes L, UC).

DISTRIBUTION. Widespread in Papua New Guinea (Madang, Morobe, Western, Milne Bay, Southern, Northern, Central and East Sepik Provinces).

NOTES. Valeton (1927) had clearly indicated the type specimen *Ledermann 9560* from Sepik, Papua New Guinea, taken during the Sepik Expedition in 1912–13. According to Van Steenis-Kruseman (1950), Ledermann's holotype collections from this expedition were deposited in the Berlin Herbarium (B) and the duplicates distributed to L, K, SING and US. The holotype of this collection was destroyed during the Second World War. The sheet from L, which is a duplicate of *Ledermann 9560*, is designated as the lectotype.

15. *Ridsdalea pseudoternifolia* (Valeton) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia pseudoternifolia* Valeton, Icon. Bogor. 4 (1912) 123, t. CCCXXXVIII. TYPE: *Teysmann 19411*, Insula Liengga, prope Sapientjan, Feb 1911 (holotype BO; isotype L). (Fig. 4)

Rothmannia kuchingensis sensu Coode et al., Checkl. Flow. Pl. & Gymn. Brunei (1996) 290, non (W.W.Smith) K.M.Wong (= *Ridsdalea grandis*).

Rothmannia schoemanii sensu Kessler et al., Checkl. Tree Flora Balikpapan-Samarinda area, East Kalimantan, Indonesia (1992) 67, non (Teijsm. & Binn.) Tirveng.

Rothmannia sp. nov. in Kessler & Sidiyasa, Trees Balikpapan-Samarinda area, East Kalimantan, Indonesia (1994) 202, fig. 16.

Rothmannia sp. 2 in Beaman & Anderson, Pl. Mt. Kinabalu 5 (2004) 340.

DISTRIBUTION. Endemic to Sumatra and Borneo (Sabah, Sarawak, Brunei & Kalimantan).

16. *Ridsdalea pulcherrima* (Kurz) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia pulcherrima* Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 41(4) (1872) 312; For. Fl. Br. Burma 2 (1877a) 43. *Randia andamanica* N.P.Balakr., nom. nov., Bull. Bot.

Surv. India 22 (1980 pub. 1982) 175. *Rothmannia pulcherrima* (Kurz) Tirveng., Nord. J. Bot. 3 (4) (1983) 469. TYPE: *Kurz s.n.*, South Andaman, sine datum (holotype CAL; isotypes K, P).

DISTRIBUTION. Andaman Islands.

17. *Ridsdalea schoemanii* (Teijsm. & Binn.) J.T.Pereira, **comb. nov.**

Basionym: *Gardenia schoemanii* Teijsm. & Binn., Nat. Tijdschr. Ned. Ind. 3 (1852) 327; Teisjm. & Binn., Catalogus van 's Lands Plantentuin te Buitenzorg (1854) 98; De Vriese & Dozy, Ned. Kruidk. Arch. 3 (1855) 403; Miq., Fl. Ind. Bat. 2 (1856) 232. *Randia schoemanii* (Teijsm. & Binn.) Bakh. f., in Backer, Bekn. Fl. Java 15 (1956) 86; Backer & Bakhuizen, Fl. Java 2 (1965) 310; Corner, Wayside Trees Malaya 2 (1988) 648. *Rothmannia schoemanii* (Teijsm. & Binn.) Tirveng., Nord. J. Bot. 3 (1983) 469; Wong, Malay. Nat. J. 38 (1984) 49; Tree Fl. Malaya 4 (1989) 406; Ng, Manual Forest Fruits, Seeds & Seedlings, Malay. For. Rec. 34 (1992) 491, Figs. 809–810; Lemmens & Wulijarni-Soetjipto, Plant Resources South-East Asia 3 (1992) 151. NEOTYPE (here designated)**:** *Koorders Kds. 6859* β, Res. Bantam (Bogor), 16 Jul 1892 (neotype BO: sheet no. BO-1334900) (isoneotype K). (Fig. 10, 11)

Fig. 10 (left). *Ridsdalea schoemanii*, open flower and young buds. (Photo: E.M. Lai) **Fig. 11** (right). View from above: branching system in *Ridsdalea schoemanii*. (Photo: J.T. Pereira)

Randia exaltata Griff., Notul. ad Plantas Asiaticas 4 (1854) 262; Kurz, For. Fl. Br. Burma 2 (1877a) 46, J. Asiat. Soc. Bengal 46 (2) (1877b) 157; Hooker, Fl. Br. India 3 (1880) 114, pro parte quoad *Kew. Dist. 2826*, excl. *Kurz* s.n. (= *Ridsdalea pulcherrima*); Koord. & Valeton, Bijdr. Booms. Java 8 (1902) 88 pro parte, excl. *Gardenia pulcherrima* Kurz in syn. (= *Ridsdalea pulcherrima*); King & Gamble, J. Asiat. Soc. Bengal 72 (1903) 214, pro parte, excl. Andaman Islands (= *Ridsdalea pulcherrima*); Brandis, Ind. Trees (1906) 383, pro parte, excl. *G. pulcherrima* in syn.; Koord., Exkursionflora Java 3 (1912) 256; Koord.-Schum., System. Verzeichen. Part I, 1 Fam 270 (1913) 84; Koord. & Valeton, Atlas der Baumarten van Java 3 (1915) Figs. 527, 528; Pitard, Fl. Gén. Indo-Chine 3 (1923) 245, pro parte, excl. *G. pulcherrima* Kurz in syn.; Ridley, Fl. Malay Penins. 2 (1923) 78; Craib, Fl. Siam. Enum. 2, 1 (1932) 101, pro parte, excl. *G. pulcherrima* in syn.; Burkill, Dictionary Econ. Prod. Malay Penins. 2 (1966) 1897. *Rothmannia exaltata* (Griff.) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7, in obs. TYPE: *Griffith 962*, Myanmar, sine datum (holotype K).

DISTRIBUTION. Myanmar, Thailand, Peninsular Malaysia, Sumatra, and Java.

18. *Ridsdalea sootepensis* (Craib) J.T.Pereira, **comb. nov.**

Basionym: *Randia sootepensis* Craib, Bull. Misc. Inform. Kew (10) (1911) 391; Fl. Siam. Enum. 2(1) (1932) 112; Pitard, Fl. Gén. Indo-Chine 3 (1923) 230. *Rothmannia sootepensis* (Craib) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs. *Rothmannia sootepensis* (Craib) T.Yamaz., J. Jap. Bot. 45 (1970) 340. TYPE: *Kerr 1651*, Thailand, Chiang Mai (holotype K; isotypes BM, TCD).

DISTRIBUTION. Thailand.

19. *Ridsdalea thailandica* (Tirveng.) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia thailandica* Tirveng., Nord. J. Bot. 3(4) (1983) 466. TYPE: *Phusomsaeng 18* (Flora of Thailand *BKF 35922*), Thailand, Ubon Ratchathani, Chong Mek, 23 Feb 1967 (holotype BKF; isotypes AAU, C, K, L).

DISTRIBUTION. Northeast Thailand.

20. *Ridsdalea uranthera* (C.E.C.Fisch.) K.M.Wong, **comb. nov.**

Basionym: *Randia uranthera* C.E.C.Fisch., Bull. Misc. Inform. Kew (10) (1929) 314; Hook. Icon. (1933) t. 3143. *Rothmannia uranthera* (C.E.C.Fisch.) Tirveng., Nord. J. Bot. 3(4) (1983) 469. TYPE: *Ba Pe per Parkinson 8108*, Burma, Tavoy, Ba Wa Forest Reserve (holotype K).

DISTRIBUTION: Myanmar, Thailand.

21. *Ridsdalea uvarioides* (Valeton) J.T.Pereira, **comb. nov.**

Basionym: *Randia macromera* var. *uvarioides* Valeton, Bot. Jahrb. Syst. 60 (1926) 91. NEOTYPE (here designated)**:** *Ledermann s.n.*, Papua New Guinea, Sepik, 1912–13 (SING).

DISTRIBUTION. Recorded so far only in Papua New Guinea (East Sepik Province).

NOTES. The var. *uvarioides* of Valeton (1926) is here raised to specific rank because it is sufficiently distinct from the typical var. *macromera*. Features distinguishing var. *uvarioides* from var. *macromera* include the glabrous to scabrid lower leaf surface in var. *uvarioides* (densely velvety hairy in var. *macromera*), longer stipules (10–23 mm long in var. *uvarioides*, 5–8 mm long in var. *macromera*), colleters inside the stipules of var. *uvarioides* that are confined to a triangular area with more than 5 rows at the central part (colleters are arranged in a narrow zone usually of 1–2 rows at sparse intervals, and along the bottom edge of the stipule base in *var. macromera*), 5–10 flowers per cyme in var. *uvarioides* (more flowers, 11–24 per cyme in var. *macromera*), and a longer corolla tube, (3.5–)4–5 cm long in var. *uvarioides* (1–1.5 cm long in var. *macromera*). Attempts have been made to locate the holotype of Ledermann's collection listed in Valeton's account from the Berlin Herbarium (where most of Ledermann's collections were kept) and duplicates in the other herbaria, i.e. L, K and SING (Van Steenis- Kruseman 1950). We could not track down any of these.

However, an unnumbered flowering collection of this species made by Ledermann in the Sepik region during the Sepik Expedition in 1912–13 (the same collecting time and area as the specimens listed in Valeton's account) was discovered at the Singapore Herbarium. This is the only specimen found which matches the original description, and is designated as the neotype for this species.

22. *Ridsdalea venalis* (Bremek.) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia venalis* Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 6, in obs. TYPE: *Vidal 798*, Laos, Vientiana, 23 Jan 1949 (holotype U; isotype P).

DISTRIBUTION. Laos.

23. *Ridsdalea vidalii* (Bremek.) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia vidalii* Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7, in obs. TYPE: *Vidal 1741*, Laos, Savannakhet, 25 May 1952 (holotype U; isotype P).

DISTRIBUTION. Laos.

24. *Ridsdalea vietnamensis* (Tirveng.) J.T.Pereira, **comb. nov.**

Basionym: *Rothmannia vietnamensis* Tirveng., Nord. J. Bot. 3(4) (1983) 469. TYPE: *Poilane 24313*, Vietnam, Annam, col de Braian Haut Douai, 14 Feb (rec. Jul) 1935 (holotype P).

DISTRIBUTION. Vietnam.

25. *Ridsdalea wittii* (Craib) J.T.Pereira, **comb. nov.**

Basionym: *Randia wittii* Craib, Bull. Misc. Inform. Kew (1911) (10): 392; Fl. Siam. Enum. 2 (1932) 114. *Rothmannia wittii* (Craib) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7, in obs. TYPE: *Witt s.n.*, Thailand, Rachasma, Korat (K, *n.v.*).

(Fig. 6B)

DISTRIBUTION. Northeast Thailand.

Singaporandia K.M.Wong, **genus novum**

This new genus is distinguished from *Rothmannia* Thunb. by its corolla lobes contorted to the left (the lobes in *Rothmannia* s.s. are contorted to the right), and from other related genera in the *Rothmannia* alliance by its distinctive plant architectural form characterized by continuous growth of the orthotropic stem axis with branch production at successive nodes, and 2-node primary branch modules in which the proximal node bears a pair of normal leaves and the distal node has complete reduction of both leaves, with only rare development of a secondary branch module by substitution growth. The new genus also differs from other Asian members of the alliance by its infundibular corolla with exceptionally long (20–25 mm) anthers and large pollen and ectocolpus (polar axis P=34 μm, equatorial diameter E=35.9 μm, ectocolpus width 7.1–11.8 μm) (the other taxa have 5–20 mm long anthers, P=26.5 μm, E=32.3 μm, ectocolpus width only up to 5 μm wide).

TYPE SPECIES: *Singaporandia macrophylla* (R.Br. ex Hook.f.) K.M.Wong

Randia sect. *Euclinia* DC., sensu Hook.f., in Benth. & Hook.f., Gen. Pl. 2 (1873) 89 pro parte & Fl. Brit. India 3 (1880) 114, pro parte quoad *R. macrophylla* R.Br.; sensu K.Schum., in Engl. & Prantl, Nat. Pflanzenf. 4, 4 (1891) 76 pro parte quoad *R. macrophylla* (R.Br.) Hook.f.

Randia sect. *Grandiflorae* Ridl., Fl. Malay Penins. 2 (1923) 71, pro parte quoad *R. macrophylla* R.Br. ex Hook.f.

Randia sensu Koord. & Valeton, Bijdr. 8 (1902) 88 & sensu King & Gamble, J. As. Soc. Beng. 72 (1903) 214–215, pro parte quoad *R. macrophylla* Benth. & Hook.f. (*sic*!).

Rothmannia pro parte quoad *R. macrophylla* sensu Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7; Wong, Malay. Nat. J. 38 (1984) 46; Wong, Tree Fl. Malaya (1989) 324; Kochummen, Tree Fl. Pasoh Forest (1997) 385.

Treelets to small trees, sometimes shrub-like plants; unarmed. ***Stem*** orthotropic with continuous production of branches. ***Branches*** opposite and decussate or only one produced at each node on the trunk, plagiotropic by substitution when a rare second module develops; terminated by inflorescence development. ***Stipules*** interpetiolar, free, persistent, inner surface hairy with 3–4 rows of colleters at the basal part; apex long-acuminate. Branch ***leaves*** in pairs at the proximal node and completely vestigial at the distal node; secondary veins 10–21 pairs. ***Inflorescence*** a compact, much-reduced cyme, 1–3-flowered. ***Flowers*** bisexual; calyx tube pubescent, velvety to hispid; calyx limb cup-shaped; calyx lobes 5–6, narrowly triangular; corolla infundibular, the tube white with maroon tinged at the base on the outside, the tube 9–15 cm long, (20–)30–55 mm wide at the throat, 3–5 mm wide at the base; speckled inside, outer surface pubescent to hispid hairy, inner surface with hairy zone covering part of the tube from below the level of the anthers; corolla lobes 5, ovate with acute apex, 2.5–5.5 cm long, 1.5–2.5 cm wide, outside pubescent on the uncovered half of the lobes, inside glabrous; anthers 5, fully included within the tube (inserted at the upper 1⁄3), 20–25 mm long; stigma fusiform, slightly ribbed when dried, style and stigma included but reaching just below the corolla mouth and the level of the anthers, style smooth, glabrous. ***Fruits*** ellipsoid, 4–7 cm long, 2–3.5 cm wide, hispid when young. ***Seeds*** ellipsoid, 5–8.5 × 6–8 mm.

NOTES. This monotypic genus is named after the island republic of Singapore, where the species is well conserved in step with a heightening awareness of the value of the remaining lowland forests. A Singapore specimen collected in 1822 is also on the type sheet in Wallich's Herbarium at Kew. Its name also recalls the historical connection to *Randia*, the genus in which the type species was first placed. In the Bukit Timah long-term dynamics study plot, the population seems stable over time, with recruitment and mortality roughly in balance (LaFrankie et al. 2005). The branching and whole-plant architecture is quite unique among the *Rothmannia* alliance and perhaps also among the Rubiaceae in general.

DISTRIBUTION. A Sundaland endemic genus, restricted to west Malesia, naturally occurring in the Malay Peninsula (Peninsular Malaysia and Singapore) and Sumatra.

1. *Singaporandia macrophylla* (R.Br. ex Hook.f.) K.M.Wong, **comb. nov.**

Basionym: *Randia macrophylla* R.Br. ex Hook.f., Fl. Brit. India 3 (1880) 114; King & Gamble, J. As. Soc. Beng. 72 (1903) 215; Ridley, Fl. Malay Penins. 2 (1923) 78; Corner, Wayside Trees Malaya 2 (1988) 648. *Rothmannia macrophylla* (R.Br. ex Hook.f.) Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60(1) (1957) 7, in obs.; Wong, Malay. Nat. J. 38 (1984)

Fig. 12. Attractive large blooms of *Singaporandia macrophylla*. (Photo: Cerlin Ng)

46; Wong, Tree Fl. Malaya (1989) 324; Kochummen, Tree Fl. Pasoh Forest (1997) 385; LaFrankie et al., Forest Trees Bukit Timah (2005) 142. LECTOTYPE (designated by Wong, 1984): Penang and Singapore, *Wallich*, *Cat*. *8304A*, 1822 (K-W).

(Fig. 12)

DISTRIBUTION. Endemic to West Malesia. It is found in Singapore, throughout Peninsular Malaysia and also in Sumatra (Jambi, Central Sumatra) and the Riau Islands.

NOTES. Although Robert Brown's name *Rothmannia macrophylla* R.Br. was used in Wallich's Catalogue (no. 8304), this was not validly published; Fagerlind (1943) had also accepted this taxon as a species of *Rothmannia* prior to Bremekamp's (1957) combination. Ridley (1923) had thought that it is closely allied to *Randia stenopetala* (=*Kochummenia stenopetala*) as both shared a similar habit (shrub) and membranous, more-or-less hairy leaves, as well as conspicuous flowers, and so he placed them in the same section, *Randia* sect. *Grandiflorae*. Wong (1984) pointed out that although the infundibular corolla shape of "*R. macrophylla*" is superficially similar to that of the type species of *Euclinia* Salisb. (*E. longiflora* Salisb.), the latter differs from *Rothmannia* s.l. species in having tetrad pollen grains instead of single grains; chaffy instead of firm stipules; and leaves clustering at the ends of twigs which are simultaneously deciduous instead of leaves at the ends of twigs and not deciduous.

As the species has large showy flowers produced regularly, Lemmens & Wulijarni-Soetjipto (1992) suggested it may be a good prospect for ornamental horticulture.

ACKNOWLEDGEMENTS

We thank the Sabah Forest Department and its Forest Research Centre, and the National Parks Board, Singapore and Singapore Botanic Gardens for support and facilities leading to the completion of these studies. Much of the morphological survey, palynological and micromorphological investigations was carried out as part of J.T. Pereira's doctoral dissertation research at the Institute of Biological Sciences, University of Malaya under the supervision of K.M. Wong and A.L. Lim. We are grateful to the late Christian Puff (University of Vienna) for much assistance with literature and images and for many highly instructive discussions on the Rubiaceae. The Keepers and Curators of the herbaria who have loaned specimens or provided information are also gratefully acknowledged. We thank Ahmad Fitri Zohari, Ang Wee Foong, Lai Ee May, Cerlin Ng, Reuben Nilus and Suzana Sabran for the use of their images. Louise Neo assisted in the preparation of Fig. 1 and 6.

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